

4-2016

# The plant phenology monitoring design for The National Ecological Observatory Network

Sarah Elmendorf

Katherine D. Jones

Benjamin I. Cook

Jeffrey M. Diez

Carolyn A. F. Enquist

*See next page for additional authors*

Let us know how access to this document benefits you.

Follow this and additional works at: [https://scholarworks.umt.edu/ntsg\\_pubs](https://scholarworks.umt.edu/ntsg_pubs)

---

## Recommended Citation

Elmendorf, S. C., K. D. Jones, B. I. Cook, J. M. Diez, C. A. F. Enquist, R. A. Hufft, M. O. Jones, S. J. Mazer, A. J. Miller-Rushing, D. J. P. Moore, M. D. Schwartz, and J. F. Weltzin. 2016. The plant phenology monitoring design for The National Ecological Observatory Network. *Ecosphere* 7(4):e01303. 10.1002/ecs2.1303

This Article is brought to you for free and open access by the Numerical Terradynamic Simulation Group at ScholarWorks at University of Montana. It has been accepted for inclusion in Numerical Terradynamic Simulation Group Publications by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact [scholarworks@mso.umt.edu](mailto:scholarworks@mso.umt.edu).

---

**Authors**

Sarah Elmendorf, Katherine D. Jones, Benjamin I. Cook, Jeffrey M. Diez, Carolyn A. F. Enquist, Rebecca A. Hufft, Matthew O. Jones, Susan J. Mazer, Abraham J. Miller-Rushing, David J. P. Moore, Mark D. Schwartz, and Jake F. Weltzin

## The plant phenology monitoring design for The National Ecological Observatory Network

SARAH C. ELMENDORF,<sup>1,2,†</sup> KATHERINE D. JONES,<sup>1</sup> BENJAMIN I. COOK,<sup>3</sup> JEFFREY M. DIEZ,<sup>4</sup> CAROLYN A. F. ENQUIST,<sup>5,6</sup> REBECCA A. HUFFT,<sup>7</sup> MATTHEW O. JONES,<sup>8</sup> SUSAN J. MAZER,<sup>9</sup> ABRAHAM J. MILLER-RUSHING,<sup>10</sup> DAVID J. P. MOORE,<sup>11</sup> MARK D. SCHWARTZ,<sup>12</sup> AND JAKE F. WELTZIN<sup>13</sup>

<sup>1</sup>The National Ecological Observatory Network, 1685 38th St., Boulder, Colorado 80301 USA

<sup>2</sup>Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA

<sup>3</sup>NASA Goddard Institute for Space Studies, 2880 Broadway, New York, New York 10025 USA

<sup>4</sup>Department of Botany and Plant Sciences, University of California, Riverside, California 92521 USA

<sup>5</sup>USA National Phenology Network, National Coordinating Office, 1955 E. 6th Street, Tucson, Arizona 85719 USA

<sup>6</sup>DOI Southwest Climate Science Center, U.S. Geological Survey, 1064 E. Lowell Street, Tucson, Arizona 85721 USA

<sup>7</sup>Denver Botanic Gardens, 909 York Street, Denver, Colorado 80206 USA

<sup>8</sup>Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331 USA

<sup>9</sup>Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA

<sup>10</sup>National Park Service, Acadia National Park and Schoodic Education and Research Center, Bar Harbor, Maine 04660 USA

<sup>11</sup>School of Natural Resources and the Environment, University of Arizona, 1064 East Lowell Street, Tucson, Arizona 85721 USA

<sup>12</sup>Department of Geography, University of Wisconsin-Milwaukee, PO Box 413, Milwaukee, Wisconsin 53201 USA

<sup>13</sup>US Geological Survey, 1955 East 6th St., Tucson, Arizona 85721 USA

**Citation:** Elmendorf, S. C., K. D. Jones, B. I. Cook, J. M. Diez, C. A. F. Enquist, R. A. Hufft, M. O. Jones, S. J. Mazer, A. J. Miller-Rushing, D. J. P. Moore, M. D. Schwartz, and J. F. Weltzin. 2016. The plant phenology monitoring design for The National Ecological Observatory Network. *Ecosphere* 7(4):e01303. 10.1002/ecs2.1303

**Abstract.** Phenology is an integrative science that comprises the study of recurring biological activities or events. In an era of rapidly changing climate, the relationship between the timing of those events and environmental cues such as temperature, snowmelt, water availability, or day length are of particular interest. This article provides an overview of the observer-based plant phenology sampling conducted by the U.S. National Ecological Observatory Network (NEON), the resulting data, and the rationale behind the design. Trained technicians will conduct regular in situ observations of plant phenology at all terrestrial NEON sites for the 30-yr life of the observatory. Standardized and coordinated data across the network of sites can be used to quantify the direction and magnitude of the relationships between phenology and environmental forcings, as well as the degree to which these relationships vary among sites, among species, among phenophases, and through time. Vegetation at NEON sites will also be monitored with tower-based cameras, satellite remote sensing, and annual high-resolution airborne remote sensing. Ground-based measurements can be used to calibrate and improve satellite-derived phenometrics. NEON's phenology monitoring design is complementary to existing phenology research efforts and citizen science initiatives throughout the world and will produce interoperable data. By collocating plant phenology observations with a suite of additional meteorological, biophysical, and ecological measurements (e.g., climate, carbon flux, plant productivity, population dynamics of consumers) at 47 terrestrial sites, the NEON design will enable continental-scale inference about the status, trends, causes, and ecological consequences of phenological change.

**Key words:** long-term monitoring; NEON; open-source data; plant phenology; sample design; Special Feature: NEON Design.

**Received** 30 July 2015; revised 6 November 2015; accepted 12 November 2015. Corresponding Editor: E.-L. Hinckley.

**Copyright:** © 2016 Elmendorf et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** selmendorf@neoninc.org

## INTRODUCTION

The overarching mission of NEON is to enable understanding and forecasting of the impacts of climate change, land use change, and the introduction of invasive species on ecosystem structure and function (see Thorpe et al., *unpublished manuscript*). Tracking the timing of seasonally recurring life cycle events (phenology) is thus a natural focal area of study for the Observatory. Plant phenological transitions may be triggered by a variety of cues, including chilling, spring temperature, growing degree days, and daylight (Chuine 2000); many of these factors are likely to shift significantly over the next 30 yr (IPCC 2013). Changes in phenology have been observed for many taxa across the earth (Parmesan and Yohe 2003). The onset of spring phenological events advanced at an estimated mean rate of 1.2 d per decade from 1955 to 2002, across the Northern Hemisphere, likely caused by recent climate warming (Schwartz et al. 2006). Observational and experimental studies indicate that plants flower on average ~5 d earlier per 1 °C increase in spring temperature (Wolkovich et al. 2012) and current projections indicate that spring phenology could advance by between 1 and 10 d over the planned 30-yr lifespan of the NEON observatory (IPCC 2013). Many species, however, delay flowering in response to increases in winter or spring temperatures (Mazer et al. 2013), and there is still much to learn about the causes of variation among species and higher taxa in the direction and magnitude of their phenological responses to both temperature and rainfall (Mazer et al. 2013, 2015).

Beyond providing an indicator of climate change, the timing of phenological transitions is also a potentially important driver of demographic trajectories and biogeographic distributions of individual taxa, and of ecological processes including species interactions and rates of biogeochemical cycling (Morissette et al. 2008). Phenological traits may physiologically constrain broad-scale distribution patterns of species; phenology is consistently an important predictor in process-based species distributions models (Chuine 2010 and references therein). Models of temperate deciduous trees, for example, indicate that the northern range limits are constrained by the ability to complete reproductive cycles

within a growing season, and the southern limit by insufficient chilling to break bud dormancy. Phenological plasticity may be a beneficial trait. Species whose activity patterns closely track interannual climate variability tend to have improved growth, productivity, or reproductive success than those that do not (Cleland et al. 2012). In other cases, however, early greenup or floral bud development in response to anomalously early arrival of spring can be detrimental. Phenological advancement in response to warm spring temperatures followed by a late frost can have catastrophic effects on fruit and seed production, and canopy development (Inouye 2008, Hufkens et al. 2012).

Climate-induced changes in phenology can create feedbacks that alter biogeochemical cycling and species interactions (Melillo et al. 2014). Changes in the timing of leaf budburst and senescence affect surface radiation, near surface temperature, hydrology, and carbon cycling (Churkina et al. 2005, Bonan 2008, Richardson et al. 2010, Jeong et al. 2012, 2013). An analysis of more than a dozen models included in the North American Carbon Program (NACP) Interim Synthesis indicated across all models, sites, and years of data, for each forest type; errors of up to 25 d in predictions of “spring onset” were common, and errors of up to 50 d were observed (Richardson et al. 2012). From the general positive relationship between carbon uptake and season length derived from a synthesis of a range of eddy covariance sites, the largest phenological errors in current models would translate into between ~150 and ~450 g/m<sup>2</sup> of carbon annually (Churkina et al. 2005). Differential responses to phenological cues between plants, consumers, and/or pollinators can disrupt the overlap in activity periods among interacting organisms, potentially resulting in changes in species fecundity and cascading effects on the food chain (Strode 2003, McKinney et al. 2012) or local extinction of consumer populations (Singer and Parmesan 2010).

Plant phenology has been studied at a range of geographic and temporal scales, and by employing a variety of tools, including: recording in situ observations, experimental manipulation of abiotic factors, modeling, remote sensing, and digital photography (Cleland et al. 2007). Understanding and reconciling the information

contributed at each scale is challenging (Morissette et al. 2008) and observations at multiple scales are rare (but see Liang et al. 2011). This article provides an overview of the plant phenology sampling that will occur within NEON sites, including observation protocols, the spatial and temporal frequency of monitoring, the taxa targeted for observations, and the rationale for the sampling regime that was selected (Box 1). The science design, developed by a technical working group comprised of phenology experts from academic institutions, government and nonprofit agencies, reflects current best practices in monitoring terrestrial plant phenology. The aims of the plant phenology monitoring dovetail with those of the NEON project more generally: to improve the understanding and forecasting of ecological change at continental scales (Schimel et al. 2011). From its earliest inception, the design of the NEON project as a whole has focused on generating core measurements that address the data needs common to the broadest possible community of data users (AIBS 2000). This differs from many site-based or PI-driven projects in that the data are intended to answer multiple questions, rather than tailored to a specific hypothesis test.

By providing integrated and multiscale suites of measurements on the seasonal progression of a diversity of taxa and ecosystem processes at intensively measured sites, data collected by NEON will enable the scientific community to develop mechanistic linkages between the

environmental drivers that affect plant phenology, as well as the functional consequences of changing phenology for a range of ecosystem types and processes. The resulting scientific knowledge can inform decision-making processes related to natural resource conservation and management, control of invasive species and infectious disease, and efforts related to societal climate change adaptation (Enquist et al. 2014).

## SAMPLING DESIGN

### *Measurements*

Plant phenology is typically quantified by observing the date of onset and the duration of particular phenophases, which may include both vegetative and reproductive events. Specific phenophase definitions have not been universally adopted across monitoring networks. Without common units, data interoperability becomes a limiting factor in data integration. Consistent with NEON's commitment to use existing scientifically accepted, vetted, and standardized protocols wherever possible, NEON will employ USA National Phenology Network (USA-NPN) phenophase definitions and protocols (Denny et al. 2014).

Advantages of USA-NPN protocols and the reasons for selecting this standard for NEON in situ phenology observations include: (1) status-based monitoring, or the practice of reporting the phenological condition of an individual at any

### **Box 1** **NEON's Contribution**

NEON is poised to advance the field of phenology by:

1. Accumulating high quality, long-term, standardized measurements recorded by trained technicians across 20 major ecosystem types found within the United States.
2. Observing replicate individuals of select species to quantify intraspecific variation in the timing of phenological events within and across years, facilitating precise population-level estimates of phenology.
3. Observing multiple species to characterize the range of phenological response patterns across species, functional groups and life history strategies.
4. Collocating plant phenological measurements with other terrestrial and atmospheric measurements data, which may be used to understand relationships between climate, phenology, ecosystem processes, and biodiversity.
5. Providing open-access, standardized data sets using common protocols and units, in order to facilitate synthetic analyses using data from NEON together with data from other large-scale monitoring networks.

time that it is monitored; (2) repeated tracking of marked and georeferenced replicate individual perennials and patches of annual/clonal herbs, and (3) incorporation of both status and “intensity” definitions for phenophases (Kao et al. 2012, Denny et al. 2014). Using status-based rather than first-event monitoring is a departure from many historical phenological monitoring protocols, but has the advantage that events (such as leaf emergence in Mediterranean climates, or flowering in many desert species) that may occur multiple times during a single year can be captured. Status monitoring also allows the explicit quantification of uncertainties in phenophase transition dates (which occur in continuous time) that are introduced by monitoring in discrete temporal bouts, as well as quantifying the duration of phenophases rather than just their date of onset. Monitoring marked individuals/small patches ensures that the recorded dates of phenological events, or their duration, are decoupled from population size (Miller-Rushing et al. 2008). Status monitoring overcomes weaknesses of event monitoring, and when coupled with a regular sampling frequency, enables more accurate phenophase change estimates. Repeated tracking of the same georeferenced individual allows the NEON phenology measurements to be used as phenoclimate monitors (like cloned lilacs; see Schwartz et al. 2012) rather than conflating variation within a population with climate effects. The protocols employed include intensity metrics (e.g., percentage of the canopy that is full with leaves) along with phenophase status (e.g., one or more live, unfolded leaves visible). These data can be used to estimate mean population onset and end dates for each phenophase, as well as track the seasonal progression of development throughout the active period. Together, these data should provide better linkages to ecosystem function and remotely sensed phenological data than existing “first event” phenological data sets, which typically quantify the phenological status of only the most extreme individuals within a population of unknown size (Miller-Rushing et al. 2008). Although other phenophase definitions exist [e.g., the BBCH scale, commonly used in agricultural systems, as well as across Europe (Meier 2001, Koch et al. 2007)], the USA-NPN scales were selected for interoperability with large-scale distributed monitoring data sets in

the continental United States. Mapping from USA-NPN definitions to BBCH definitions is feasible for many phenophases (Denny et al. 2014).

The phenology protocol includes repeated assessment of phenophase status and intensity on each individual (see section Temporal distribution of sampling, below, for more details), as well as an annual assessment of individual-level covariates that can affect phenology. Due to resource constraints, only a subset of the USA-NPN-defined phenophases (as described by Denny et al. 2014) will be targeted in NEON phenology sampling protocols, with the greatest focus on leaf phenology. The focus on canopy development was selected, based on recommendations of a NSF Research Coordination Network (USA-NPN National Coordinating Office 2012), to facilitate linkages with NEON’s measurements of ecosystem processes such as landscape phenology and carbon cycling. To connect phenological measurements to plant health, productivity, and canopy position, NEON will measure the size (stem diameter, % cover, height, and canopy dimensions), disease status, health condition, and structure of each individual plant or patch once per year. These annual measurements will be consistent with those taken on other plants in the network as part of NEON’s vegetation structure and productivity protocol (see Meier and Jones 2015 for details).

#### *Phased sampling design*

Two priorities were identified for NEON’s plant phenology observations: *Phenology of dominants*, which includes estimating the mean and intraspecific variance of phenological timing in dominant species within each site (see Phase I, below), and *Community phenology*, focused on capturing a range of species-specific phenologies that represent the plant community at each NEON site (Phase II). Dominants are targeted specifically to facilitate linkages to ecosystem function based on the assumption that species contribute to ecosystem properties roughly in proportion to their relative abundances (Grime 1998). Sampling of dominant species’ phenology will enable linking phenological events and patterns observed to aboveground processes captured at other scales by other NEON measurement systems (including ecosystem productivity and respiration, and carbon, water, and nutrient cycling), and to the ground-based land-surface phenology signal

observed via remote sensing methods. It will also provide critical information on intraspecific variation in phenology patterns, which are poorly captured when monitoring efforts are limited to a census of one to several individuals per site. Sampling of community-level phenology will inform questions regarding interspecific variation in the timing and duration of phenological phases, and their sensitivity to climate. The resulting data set will enable assessment of the degree to which phenological timing and climate sensitivity vary based on functional groups or growth forms (e.g., natives/exotics, overstory/understory, perennial/annual, deciduous/evergreen, herbaceous/woody, early and late-season). These patterns can enable generalizations regarding the likely phenological responses and sensitivities of species beyond those targeted for regular observation.

NEON will implement phenological monitoring in two phases in order to accomplish both inter- and intra-specific sampling goals. During Phase I (phenology of dominants), implemented during the first three full (i.e., all sites operational) years of sampling, phenological observations will concentrate on intensive monitoring of three dominant species at each of the 47 terrestrial sites. The NSF Research Coordination Network (RCN) report (USA-NPN National Coordinating Office 2012) recommends a minimum of 5–10 replicate individuals sampled for vegetative phenology per site per species, with an ideal sampling intensity of 20–30 individuals. In the absence of existing data sufficient to statistically determine smaller minimum sample sizes for particular species and sites, NEON will target the higher end of this range in order to quantify intraspecific variation in phenological timing for the three most dominant species at each site (see section Temporal distribution of sampling, below, for details of monitoring frequency).

Phase II (community phenology), will follow Phase I and consist of more limited sampling than Phase I in terms of frequency and the number of replicate individuals per species (minimum of five individuals per species per site), but will have an increased number of species. The focal shift will alter which individuals are monitored, but keep the total number of plants monitored per site at ~90–100 due to budgetary limitations. Phase II monitoring will commence

in the 4th year of operational sampling and will continue for the remainder of NEON operations at each site. Species to be monitored in Phase II will include dominant species (the three species studied as part of Phase I at each site) and up to 17 additional species per site that collectively represent a range of functional groups and life history strategies. Phase II will inform both the range of phenological patterns occurring at a site, as well as predictive models of the sensitivities of particular species based on their traits (Buckley and Kingsolver 2012).

#### *Spatial distribution of sampling*

A common critique of much of the existing ground-phenology observation data is that observations are limited in space and are reported as points, whereas remote sensing data pixels from commonly used satellite products used to model phenology range from 30 m to >1 km (Schwartz and Hanes 2010). While some studies have found little spatial autocorrelation in a single plant species' phenological response given uniform temperature over small areas (Schwartz et al. 2014), dispersion of monitored individuals throughout a larger area is important to encompass variation in plant phenology within the sampling area caused by microenvironmental variation, genetic variation, or both. To facilitate repeatable observation of multiple individuals over a relatively large area, while keeping travel time to a minimum, marked individuals will be situated along a fixed, 800-m square "loop" transect (200 m on a side), with the four edges oriented in the four cardinal directions. This size is comparable to the ~250 m MODIS pixel size, which is commonly used in satellite-based phenology assessments.

This loop will be situated within or near NEON's flux tower airshed. The distance of the transect from the tower will be site specific based on identified exclusion areas around tower instrumentation, and will be placed to facilitate inclusion of individuals located within sampling plots used for NEON's biomass and productivity measurement (see Meier and Jones 2014) (Fig. 1). Collocation of the phenology transect with the instrument tower will allow meteorological and biophysical data collected by tower-mounted sensors to be used directly in analysis of phenological data (e.g., how local climate affects

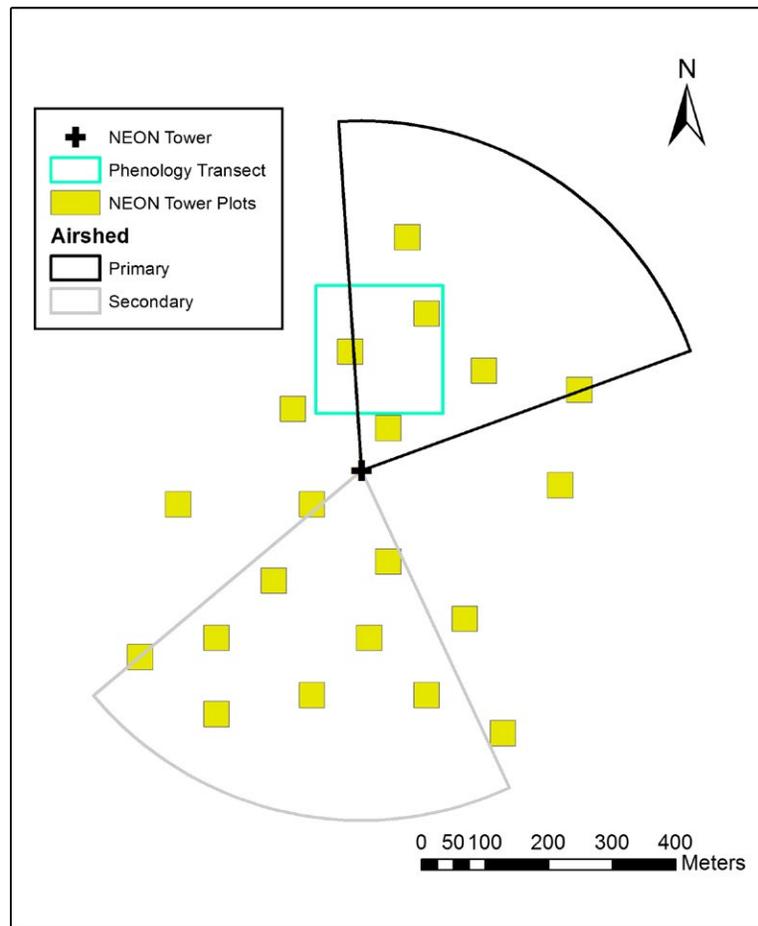


Fig. 1. Layout of phenology transect (teal square) with respect to the NEON Tower (cross shape), the airshed (wedge shapes), and the Tower Plant Productivity plots (yellow squares) (figure credit: Rachel Krauss, 2015).

phenology) and vice versa (e.g., how leaf status affects daily carbon flux). NEON's tower locations are positioned such that the tower airshed is situated in a spatially and structurally homogeneous area with the goal of a minimum of 80% contribution from the representative ecosystem, ensuring that plants selected for phenological monitoring are also located within a regionally representative habitat type. The assumption is that the intraspecific variation in phenological responses will, in general, be from individuals subject to similar environmental conditions. Even so, microtopographic features may still affect variation in observed phenological response. Additional information such as slope, aspect, community composition, above-ground biomass, and canopy chemistry as derived from NEON's airborne observation system may provide

additional insight into the realized environmental heterogeneity of the various sites.

#### *Temporal distribution of sampling*

A standard sampling frequency for phenology has not been prescribed by the ecological community. Typically, sampling frequency varies by species, environment, sampling objectives, and budgetary and logistical constraints. Accuracy of measurements can be improved by either increased precision of measurements (i.e., more frequent sampling or more extensive training) or by increased sample size (Nguyen et al. 2009). Phenophase status assessment using USA-NPN definitions shows good interobserver agreement, with volunteers classifying plants into the same phenophase as professional botanists 91% of the time (Fuccillo et al. 2014), a number which

should increase for trained NEON technicians. Variability in phenology is seen across a wide range of scales, including differences between ecosystems, sites, plots, species, and individuals (Diez et al. 2012, 2014). Therefore, the ideal frequency of sampling depends on analysis goals (e.g., fitting a thermal forcing model vs. long-term trend detection vs. quantifying intraspecific variation in phenology), as well as the degree of intraspecific and interannual variation in phenology. Mazer et al. (2015) found that twice-weekly sampling over a 3-yr period was sufficient to detect statistically significant associations between winter monthly rainfall and/or mean temperature (and their interactions), and the onset dates of vegetative growth, flowering, and fruiting in four species monitored in California across broad environmental conditions. An NSF Research Coordination Network (RCN) report on phenology (2012) suggests a sampling interval of 2–4 times per week. Miller-Rushing et al. (2008) recommend sampling every second day to ensure a 97% chance of detecting a significant change in flowering date over 10 yr of sampling, based on existing long-term flowering data collected in Massachusetts and Colorado. These recommendations assumed realistic anticipated rates of climate warming and interannual variability in temperature, in addition to a sensitivity of flowering date to temperature of 1 d/°C. A more recent synthesis of long-term phenology data sets worldwide (Wolkovich et al. 2012), however, suggests that flowering phenology will, on average, shift at a rate of 5–6 d/°C. Therefore, less frequent sampling may be adequate for many species for simple trend detection.

Following the RCN recommendations, during the first 3 yr of sampling, the phenological status of dominant species (Phase I) will be observed three times a week during key transition periods (i.e., leaf emergence and senescence, Table 1). Resulting data will be used to inform the sampling intensity necessary to characterize the mean ( $\pm 3$  d SE) for leaf phenology transition dates for the three dominant species at the site in subsequent years. This target is based on an analysis by Jeong et al. (2012), who concluded that when observational error in estimating population mean transition days for key phenological events (e.g., budbreak) is greater than  $\pm 3$  d, parameter-

izing phenological forcing models is compromised. During Phase II, the frequency of phenological observations will be reduced to two times a week during transitional phases in order to accommodate sampling of a greater number of species.

Phenologically active periods will vary among species both spatially across the continent, and interannually at each site. In order to catch the full growing season for all selected species, NEON will aim to commence weekly sampling 3 weeks prior to the earliest anticipated onset of the first phenophase (based on the earliest date observed in recent records for the species). This date will be determined using local information, where available (such as at LTER sites where historical phenological data exist, or indicator plants at a nearby, lower elevation site), or from historical MODIS data, in sites where local information is not available to guide sampling. Start of season metrics based on remote sensing data are typically biased towards early dates (White et al. 2009, Ganguly et al. 2010), so this should provide an “earliest” outer bound on start of season.

Once budbreak or initial growth is observed, the observation frequency will increase from once a week to either three times (Phase I) or two times (Phase II) a week. The intensive sampling stage ends once full-sized leaves have emerged/full canopy has formed, and sampling frequency is reduced to once a week or once every other week to survey for open flowers. Three weeks before the anticipated first date of senescence, based on local and/or MODIS data, sampling frequency will increase again to weekly (if previously reduced to every other week). At the first sign of leaf senescence (i.e., fall color), observation frequency will, once more, increase to two times a week sampling until <5% of leaves remain or until three consecutive censuses of no change have been observed.

### *Species selection*

Species selection is guided by several overarching principles: (1) The focus of NEON sampling is to characterize the ecology of the site. Therefore, an effort is made to sample species that are representative of the plant community at each site. (2) High level requirements of the NEON project focus on invasive species as a driver of ecological change and

Table 1. Proposed rule sets for specific growth forms for phenology sampling at sites with a well-defined growing season†.

Growth form	Monitor indicator individual for	Sample 3×/week‡ until all plants show	Sample 1×/week until all plants show	Then§	Then	Sample 2×/week until all plants show	Sample 1×/week until	Then
Cactus	Breaking flower buds	NA	No more fresh flowers	End sampling season	NA	NA	NA	NA
Deciduous broadleaf	Breaking leaf or flower buds	>50% of canopy full with leaves or three consecutive bouts of no change	≥95% of canopy full with leaves	Commence every other week monitoring for open flowers	Monitor indicator individuals for one or more colored leaves	One or more colored leaves	<5% of canopy full with green or colored leaves	End sampling season
Deciduous conifer	Breaking needle buds	>50% of canopy full with needles or three consecutive bouts of no change	≥95% or more of canopy full with needles	Commence every other week monitoring for open pollen cones	Monitor indicator individuals for one or more colored needles	One or more colored needles	<5% of canopy full with green or colored needles	End sampling season
Drought deciduous broadleaf	Breaking leaf buds	Young leaves	No more young leaves	Commence every other week monitoring for open flowers	Monitor indicator individuals for one or more colored leaves§	One or more colored leaves	<5% of canopy full with green or colored leaves	End sampling season
Evergreen Broadleaf	Breaking leaf buds	Young leaves	No more young leaves	Commence every other week monitoring for open flowers	End sampling season when no more fresh flowers are present	NA	NA	NA
Evergreen conifer	Breaking needle buds	Young needles	No more young needles	Commence every other week monitoring for open pollen cones	End sampling season when no more fresh pollen cones are present	NA	NA	NA
Evergreen forb	Breaking leaf buds	Young leaves	No more young leaves	Commence every other week monitoring for open flowers	End sampling season when no more fresh flowers are present	NA	NA	NA

Table 1 (Continued)

Growth form	Monitor indicator individual for	Sample 3×/week‡ until all plants show	Sample 1×/week until all plants show	Then§	Then	Sample 2×/week until all plants show	Sample 1×/week until	Then
Forb	Initial growth	One or more fully unfolded leaves	NA	Commence every other week monitoring for flowering phenology	Monitor indicator individuals evidence of senescence	NA	No more full-sized leaves are present	End sampling season
Graminoid	Initial growth	>50% of plant is green or three consecutive bouts of no change	≥95% of plant is green	Commence every other week monitoring for flowering phenology	Monitor indicator individuals for >5% leaf senescence	<95% green leaves	<5% of plant is green	End sampling season
Pine	Emerging needles or pollen cone development	Young needles	No young leaves	Commence every other week monitoring for open pollen cone	End sampling season when no more fresh pollen cones visible	NA	NA	NA
Semi-evergreen broadleaf¶	Breaking leaf or flower buds	Young leaves OR >50% of canopy full with leaves OR three consecutive bouts of no change	No more young leaves OR 95% or more of canopy is full with leaves	Commence every other week monitoring for open flowers	Monitor indicator individuals for one or more colored leaves#	One or more colored leaves	<5% of canopy full with green or colored leaves	End sampling season

† This is generally applicable to temperate or boreal systems; sites lacking a distinct growing season where growth occurs year round or is episodic such that a growing season cannot be defined will be monitored on a weekly basis.

‡ Three times a week in Phase I sampling, two times a week in Phase II.

§ If flowering phenology precedes leaf/needle budbreak skip the steps outlined in this column and decrease monitoring to watching indicator individuals for fall senescence or end monitoring for the season as specified in the following column.

¶ Semievergreen broadleaf growth form may be used for species in which life history varies with latitude. Monitoring strategy should be driven by phenophase observations.

# Seasonal monitoring may end at this point if senescence does not occur.

data integration with other large-scale monitoring projects. These goals dictate a particular focus on invasive species and taxa that are the focus of more widely distributed phenological monitoring. (3) The long-term nature of NEON monitoring, and a commitment to minimal site disturbance, requires that any taxa selected for monitoring be present in sufficient numbers

along an established route to sample reliably without extensive trail-building. To meet these goals, the taxa selected for plant phenology monitoring include (Phase I) three dominant species from each site, plus (Phase II) up to 17 additional taxa. Phase II species selections first targets noxious weeds and species that are the focus of other national phenological

monitoring programs, with the remaining species selected based on rank abundance.

Prior to commencing phenology observations at a given site, NEON will conduct quantitative vegetation surveys within 20–30 randomly placed plots within the tower airshed to assess site-specific species abundances. These baseline vegetation surveys are collected according to NEON's standard protocols for plant diversity and vegetation structure (Barnett 2015, Meier and Jones 2015), and are used to inform implementation details for both the phenology and vegetation structure measurements at NEON sites. Within each surveyed plot, abundance of overstory species is quantified via basal area per species, and the abundance of understory species is quantified by percent cover. Three dominant species will be identified at each site for Phase I phenology monitoring. The dominant species selected will include the two most abundant canopy species plus the single most abundant understory species for sites with >50% canopy closure, and the two most abundant understory species plus the single most dominant overstory species for sites with <50% canopy closure. At sites with no defined woody overstory, e.g., grasslands, all three species will be selected from the herbaceous community. Understory and canopy species frequently occupy discrete temporal niches, with the understory species, or in some cases understory individuals, showing advanced phenology relative to that of canopy-forming individuals (Richardson and O'Keefe 2009).

Additional species to be sampled for Phase II include up to two invasive species, and up to 5 USA-NPN "campaign taxa" and/or Project Budburst (PBB) "10 most wanted" species, with the remaining 10 species at each site picked based on rank abundance. These exceptions to the rank abundance selection process are made to intentionally target species that either contribute to NEON's ability to address its invasive species grand challenge questions or contribute to NEON's ability to align data collection with existing national citizen science data collection efforts (USA-NPN and PBB taxa). The large number of species selected should ensure that a diversity of plant growth forms, invasives, and natives are selected at sites where they are present, without requiring any a priori definition of "functional group", a concept which is not yet well under-

stood for predicting phenology. It will also serve to concentrate monitoring efforts on species that are relatively common locally, complimenting targeted selection of campaign species which have large geographic ranges and concentrate monitoring efforts on taxa that cover multiple sites.

#### *Site-specific modifications*

Modifications will be made for sites with growing seasons or species with life histories that differ from the typical temperate deciduous model. For example, sampling may begin earlier than described above to capture flowering phenophases for plants that flower prior to leaf production. Additionally, sampling frequency will need to be modified at sites without a clear seasonal greening pattern (e.g., tropical ecosystems or Mediterranean climates where species may leaf out or flower multiple times per year in response to episodic rainfall); in these cases, year-round sampling with longer intercensus intervals will be necessary to capture phenological trends. Modifications will also need to be made for cropped (agricultural) sites. At these sites, NEON will monitor the cultivated species; in most cases, the selected species will vary by year to track crop rotations and will likely not have the diversity to support Phase II sampling. Details of monitoring, including frequency and replication, may be adjusted based on the initial data collected at each site and budgetary constraints. All site specific details including site-specific modifications, species selection, and targeted sampling windows will be captured, tracked, and made available to end users as part of the NEON phenology sampling protocol (available through the NEON web portal; [www.neonscience.org](http://www.neonscience.org)).

#### *Applications of phenology data*

NEON plant phenology data will provide foundational information about the variability in plant phenology across populations, communities, and landscapes, which can be used to validate remotely sensed land-surface phenology products, and parameterize land-surface models. Accurate representation of intra- and inter-annual variability in vegetation phenology is critical for correctly predicting net CO<sub>2</sub> uptake (Desai 2010). Estimates of the vegetation

start of season and end of season, key parameters in most land-surface models, are typically derived from remote sensing estimates or physiological models based on chilling and forcing units (e.g., degree days). However, most satellite-derived phenology estimates have not been validated using ground data (Fisher and Mustard 2007), and realistic parameterization of physiologically based phenological models for wild species is limited to the very few species for which relevant data are available (Jeong et al. 2012). An evaluation of vegetation phenology in 14 terrestrial biosphere models found that for deciduous forests an early start of season bias of 2 weeks or more was typical across all models which resulted in a 13% over estimate of gross ecosystem productivity (Richardson et al. 2012). Such misrepresentation of phenology has consequences beyond ecosystem productivity estimates. When terrestrial and atmospheric models are not properly coupled, reductions in temperature associated with the onset of leaf emergence and associated increases in transpiration are often misrepresented (Levis and Bonan 2004). This insufficient coupling during critical phenological stages can lead to errors in modeled microclimate and weather patterns, and thus present cascading effects on other model components. High quality, long-term, standardized phenological measurements across major ecosystem types will be critical components for improving model development and accuracy.

Quantifying the range of phenological responses across a diversity of species and sites will aid in upscaling phenology measurements from the level of individual plants to communities and ecosystems. One approach to upscaling phenological data is through the development of more accurate phenological forcing models, as well as quantifying the uncertainty in phenology estimated from such models for sites and locations where direct measurements are not available. Bayesian hierarchical models are a promising avenue forward in community phenology forecasting (see Ibáñez et al. 2010, Diez et al. 2012, for examples, applied to individual sites with multiple taxa, or single taxa measured across multiple sites). Hierarchical models can be leveraged to generate predictions for new species or locations, as well as uncertainties on

those predictions (Gelman and Hill 2007). Multisite, multispecies data sets, as well as extensive local-scale climatological data are required for these types of models. NEON will expand the taxonomic representation of phenological data, measuring as many as 20 plant species at each of 47 sites outfitted with sensors that measure biophysical parameters. These data can form the basis of an expanded phenological modeling framework across taxa and ecosystems.

A second avenue for upscaling phenological measurements at NEON sites is using in situ measurements to validate or calibrate phenological measurements taken at broader spatial scales (e.g., phenocam- or satellite remote sensing based-phenometrics). Successful scaling from ground observations to larger spatial scales typically involves weighting species-specific phenology measurements by their coverage on the landscape (see Liang et al. 2011, 2014, Melaas et al. 2016). Colocated plot-based measurements of vegetation cover and structure, as well as vegetation maps that can be built from NEON's high-resolution hyperspectral and LiDAR remote sensing data sets make NEON sites particularly well-suited to refining this type of scaling and developing similar routines that can be applied in a diversity of ecosystem types. In addition to the human-based observations detailed here, NEON will collect landscape images multiple times per day using stationary cameras (phenocams) mounted on each flux tower. These data give a digital record of the seasonality of greening and browning over larger scales. For maximal interoperability, NEON phenocam installation and programming follows the PhenoCam Network protocols (Richardson and Klosterman 2015). Additional information on the timing of plant phenology can be informed by NEON's bi-weekly collection of leaf area index (LAI) digital hemispherical photos within the tower airshed and carbon flux estimates processed at half-hour intervals from the instrumented tower. These data streams, augmented with annual submeter hyperspectral and LiDAR remote sensing data will be valuable in determining statistical and mechanistic associations between aboveground, belowground, and landscape scale seasonal dynamics.

An ultimate goal includes not only upscaling of ground-based measurements but also using

both ground- and larger scale measurements to down-scale from larger scale greening indices to guide local-scale decision-making. Phenological data are used in a number of natural resource management activities (Enquist et al. 2014). Accurate phenological forecasts or real-time phenological tracking can aid land managers in timing controlled burns, mechanical harvesting, pesticide, and/or herbicide applications for maximum efficiency in controlling invasive species. Data on seasonal growth and senescence patterns can inform wildfire predictions. Similarly, information on peak flowering and leaf color change dates can help promote and plan for seasonal tourism coincident with wildflower or fall foliage viewing. Last, recent studies theorize that a species' ability to make appropriate phenological adjustments to a changing climate may be predictive of its future success in a changing climate (Willis et al. 2010, Pau et al. 2011). This suggests that an improved understanding of species-specific phenological sensitivities could be used to identify particularly vulnerable native taxa for protection, or prioritize invasive species for removal.

The dominant species in all plant communities generally represent key resources for animals that depend on them for food or shelter. Consequently, phenological shifts in the onset, duration, and abundance of vegetative and reproductive resources detected by phenological monitoring program can alert resource managers of changes that may affect the community composition, population dynamics, and persistence of insects, pollinators, birds, and mammals at site or regional scales. This goal requires monitoring of the animals that interact with the focal plant species at NEON sites. In addition to the plant phenology observations described here, terrestrial protocols that contribute to phenological monitoring at NEON sites include trapping of (1) mosquitoes and (2) small mammals throughout the active growing season. These data may be used to quantify phenology of mosquito emergence and annual population dynamics and small mammal reproductive periods, respectively (Thibault 2014, Hoekman et al. in press). Integration of NEON phenology data with surveillance data on other taxa, conducted either by NEON or by PIs working at NEON sites, can help track

phenological asynchrony between interacting species and potential consequences to shifts in overlapping activity periods throughout the duration of the observatory.

The development of integrated, interoperable data sets will enhance the utility of data collected by NEON and other programs. A number of other programs (e.g., USA National Phenology Network (<https://www.usanpn.org/>), Project Budburst ([budburst.org](http://budburst.org)), Long Term Ecological Research (LTER) Network sites (<http://www.lternet.edu/>), National Parks (<http://science.nature.nps.gov/im/monitor/>), the Pan European Phenology Project (PEP725; <http://www.pep725.eu/>)), as well as multiple long-term, PI-directed research projects also take phenology measurements. NEON data will augment and compliment these efforts, providing replication and longevity of measurements that are difficult to achieve without a centralized source of funding. Because of NEON's planned infrastructure, its potential to link ground-based measurements, landscape green-up and brown-down metrics, and ecosystem processes is unique (Keller et al. 2008).

One limitation of the NEON design for phenology is that the financial and logistical commitment required to measure phenology alongside a large suite of other parameters (see Lunch (2014) for the full list of NEON data products) constrains the total number of NEON sites. As a result, NEON sites are spatially sparse compared to continent-wide citizen science observation efforts, such as the USA-NPN, Project BudBurst and affiliated national and regional monitoring networks. Because NEON uses nationally standardized protocols, however, data from the intensively studied NEON sites can be readily combined with existing and ongoing efforts to facilitate continental-scale analysis and forecasting. To further this effort, an international group of phenology researchers and computer scientists is developing an ontology for plant ontology, with the aim of annotating diverse datasets to facilitate data discovery and integration. By combining ground-based observations with other North American plant phenological monitoring programs, existing data sets (e.g., Wolkovich et al. 2012), the PhenoCam network (<http://phenocam.sr.unh.edu/webcam/>), satellite imagery (e.g., MODIS land cover dynam-

ics <http://modis.gsfc.nasa.gov/data/dataproduct/>), and/or models, in situ phenology observations made by NEON can contribute important inputs to an annual “green wave” (Schwartz 1998, Ault et al. 2015) projection over the continent. On a more local scale, phenology field observations, phenocams, remote sensing, and temperature and precipitation data can be used together to understand the drivers of phenology of regionally important plant species to improve range management practices (Browning et al. 2015).

Changes in plant phenology are widely regarded as “fingerprints of climate change” or “climate change indicators” (e.g., U.S. Environmental Protection Agency 2014); indeed, plant phenology is an exemplary essential species trait in the ongoing development of Essential Biodiversity Variables (EBV’s) targeted for international monitoring (Pereira et al. 2013). Many of the meteorological and atmospheric measurements at NEON sites are Essential Climate Variables (Bojinski et al. 2014) and could facilitate empirical understanding of ecological responses to change. Ongoing efforts both nationally and internationally (e.g., PEP725), will continue to document patterns of plant phenology over large spatial extents. Leveraging data from NEON will enable the extrapolation not only of patterns of plant phenological shifts across the continent (e.g., Ault et al. 2011, Jeong et al. 2013), but potentially also of the functional consequences of these shifts. Collocated measurements conducted by NEON will elucidate the degree to which plant phenological status is broadly indicative of related ecosystem processes for which continent-wide data are sparse, such as below-ground phenology, carbon flux, seasonal biomass accumulation. In turn, the analysis, synthesis, and application of phenological information will facilitate decision-making related to critical ecological issues that affect societal well-being now and into the future.

## ACKNOWLEDGMENTS

We thank Shirley Papuga, Yuri Springer, and Lee Stanish for helpful comments on the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This material

is based upon work supported by the National Science Foundation under Cooperative Service Agreement EF-1029808.

## LITERATURE CITED

- AIBS. 2000. Report to the National Science Foundation from the second workshop on the development of a National Ecological Observatory Network (NEON). San Diego Supercomputer Center, La Jolla, California, USA, March 9-13 2000. Available online at [http://ibracs.aibs.org/reports/pdf/NEON2\\_Mar2000.pdf](http://ibracs.aibs.org/reports/pdf/NEON2_Mar2000.pdf)
- Ault, T. R., A. K. Macalady, G. T. Pederson, J. L. Betancourt, and M. D. Schwartz. 2011. Northern hemisphere modes of variability and the timing of spring in western North America. *Journal of Climate* 24:4003–4014.
- Ault, T. R., M. D. Schwartz, R. Zurita-Milla, J. F. Weltzin, and J. L. Betancourt. 2015. Trends and natural variability of spring onset in the coterminous United States as evaluated by a new gridded dataset of spring indices. *Journal of Climate* 28:8363–8378.
- Barnett, D. 2015. TOS protocol and procedure: plant diversity sampling. NEON document # NEON.DOC.014042. Available online at: <http://data.neoninc.org/documents>.
- Bojinski, S., M. Verstraete, T. C. Peterson, C. Richter, A. Simmons, and M. Zemp. 2014. The concept of essential climate variables in support of climate research, applications, and policy. *Bulletin of the American Meteorological Society* 95:1431–1443.
- Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444–1449.
- Browning, D. M., A. Rango, J. W. Karl, C. M. Laney, E. R. Vivoni, and C. E. Tweedie. 2015. Emerging technological and cultural shifts advancing drylands research and management. *Frontiers in Ecology and the Environment* 13:52–60.
- Buckley, L. B., and J. G. Kingsolver. 2012. Functional and phylogenetic approaches to forecasting species’ responses to climate change. *Annual Review of Ecology, Evolution, and Systematics* 43:205–226.
- Chuine, I. 2000. A unified model for budburst of trees. *Journal of Theoretical Biology* 207:337–347.
- Chuine, I. 2010. Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3149–3160.
- Churkina, G., D. Schimel, B. H. Braswell, and X. Xiao. 2005. Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biology* 11:1777–1787.
- Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in

- response to global change. *Trends in Ecology & Evolution* 22:357–365.
- Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. *Ecology* 93:1765–1771.
- Denny, E. G., K. L. Gerst, A. J. Miller-Rushing, G. L. Tierney, T. M. Crimmins, C. A. Enquist, P. Guertin, A. H. Rosemartin, M. D. Schwartz, and K. A. Thomas. 2014. Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. *International Journal of Biometeorology* 58:591–601.
- Desai, A. R. 2010. Climatic and phenological controls on coherent regional interannual variability of carbon dioxide flux in a heterogeneous landscape. *Journal of Geophysical Research* 115:G00J02.
- Diez, J. M., I. Ibáñez, A. J. Miller-Rushing, S. J. Mazer, T. M. Crimmins, M. A. Crimmins, C. D. Bertelsen, and D. W. Inouye. 2012. Forecasting phenology: from species variability to community patterns. *Ecology Letters* 15:545–553.
- Diez, J. M., I. Ibáñez, J. A. Jr Silander, R. Primack, H. Higuchi, H. Kobori, A. Sen, and T. Y. James. 2014. Beyond seasonal climate: statistical estimation of phenological responses to weather. *Ecological Applications* 24:1793–1802.
- Enquist, C. A., J. L. Kellermann, K. L. Gerst, and A. J. Miller-Rushing. 2014. Phenology research for natural resource management in the United States. *International Journal of Biometeorology* 58:579–589.
- Fisher, J. I., and J. F. Mustard. 2007. Cross-scalar satellite phenology from ground, Landsat, and MODIS data. *Remote Sensing of Environment* 109:261–273.
- Fuccillo, K. K., T. M. Crimmins, C. E. de Rivera, and T. S. Elder. 2014. Assessing accuracy in citizen science-based plant phenology monitoring. *International Journal of Biometeorology* 59:917–926.
- Ganguly, S., M. A. Friedl, B. Tan, X. Zhang, and M. Verma. 2010. Land surface phenology from MODIS: characterization of the Collection 5 global land cover dynamics product. *Remote Sensing of Environment* 114:1805–1816.
- Gelman, A., and J. Hill. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, New York, New York, USA.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86:902–910.
- Hoekman, D., et al. in press. Design for mosquito abundance, diversity, and phenology sampling within the National Ecological Observatory Network.
- Hufkens, K., M. A. Friedl, T. F. Keenan, O. Sonnentag, A. Bailey, J. O’Keefe, and A. D. Richardson. 2012. Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change Biology* 18:2365–2377.
- Ibáñez, I., R. B. Primack, A. J. Miller-Rushing, E. Ellwood, H. Higuchi, S. D. Lee, H. Kobori, and J. A. Silander. 2010. Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3247–3260.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.
- IPCC. 2013. Summary for Policymakers. Pages 3–29 in T. F. Stocker, D. Qin, G. K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Jeong, S.-J., D. Medvigy, E. Shevliakova, and S. Malyshev. 2012. Uncertainties in terrestrial carbon budgets related to spring phenology. *Journal of Geophysical Research* 117:G01030.
- Jeong, S.-J., D. Medvigy, E. Shevliakova, and S. Malyshev. 2013. Predicting changes in temperate forest budburst using continental-scale observations and models. *Geophysical Research Letters* 40:619–632.
- Jolly, W. M., R. Nemani, and S. W. Running. 2005. A generalized, bioclimatic index to predict foliar phenology in response to climate. *Global Change Biology* 11:619–632.
- Kao, R. H., C. M. Gibson, R. E. Gallery, C. L. Meier, D. T. Barnett, K. M. Docherty, K. K. Blevins, P. D. Travers, E. Azuaje, and Y. P. Springer. 2012. NEON terrestrial field observations: designing continental-scale, standardized sampling. *Ecosphere* 3:115.
- Keller, M., D. S. Schimel, W. W. Hargrove, and F. M. Hoffman. 2008. A continental strategy for the National Ecological Observatory Network. *Frontiers in Ecology and the Environment* 6:282–284.
- Koch, E., E. Bruns, F. M. Chmielewski, C. Defila, W. Lipa, and A. Menzel. 2007. *Guidelines for plant phenological observations*. World Climate Data and Monitoring Programme, Geneva, Switzerland.
- Levis, S., and G. B. Bonan. 2004. Simulating spring-time temperature patterns in the community atmosphere model coupled to the community land model using prognostic leaf area. *Journal of Climate* 17:4531–4540.
- Liang, L. A., M. D. Schwartz, and S. L. Fei. 2011. Validating satellite phenology through intensive ground observation and landscape scaling in a

- mixed seasonal forest. *Remote Sensing of Environment* 115:143–157.
- Liang, L., M. D. Schwartz, Z. Wang, F. Gao, C. B. Schaaf, B. Tan, J. T. Morisette, and X. Zhang. 2014. A cross comparison of spatiotemporally enhanced springtime phenological measurements from satellites and ground in a northern U.S. mixed forest. *IEEE Transactions on Geoscience and Remote Sensing* 52:7513–7526.
- Lunch, C. 2014. NEON Level 1, Level 2 and Level 3 Data Products Catalog. NEON document # NEON.DOC.002652. Available online at: <http://www.neoninc.org/>
- Mazer, S. J., S. E. Travers, B. I. Cook, T. J. Davies, K. Bolmgren, N. J. B. Kraft, N. Salamin, and D. W. Inouye. 2013. Flowering date of taxonomic families predicts phenological sensitivity to temperature: implications for forecasting the effects of climate change on unstudied taxa. *American Journal of Botany* 100:1–17.
- Mazer, S. J., K. L. Gerst, E. R. Matthews, and A. Evenden. 2015. Species-specific phenological responses to winter temperature and precipitation in a water-limited ecosystem. *Ecosphere* 6:98.
- McKinney, A. M., P. J. CaraDonna, D. W. Inouye, B. Barr, C. D. Bertelsen, and N. M. Waser. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology* 93:1987–1993.
- Meier, U. 2001. Growth stages of mono- and dicotyledonous plants. BBCH Monograph. Federal Biological Research Centre for Agriculture and Forestry, Germany.
- Meier, C., and K. Jones. 2014. TOS science design for plant biomass, productivity, and leaf area index. NEON document # NEON.DOC.000914. Available online at: <http://data.neoninc.org/documents>.
- Meier, C., and K. Jones. 2015. TOS protocol and procedure: measurement of vegetation structure. NEON document # NEON.DOC.000987. Available online at: <http://data.neoninc.org/documents>.
- Melaas, E. K., M. A. Friedl, and A. D. Richardson. 2016. Multi-scale modeling of spring phenology across Deciduous Forests in the Eastern United States. *Global Change Biology* 22:792–805.
- Melillo, J. M., T. Richmond, and G. W. Yohe, editors. 2014. Climate change impacts in the United States: the third national climate assessment. U.S. Global Change Research Program, Washington, D.C., USA.
- Miller-Rushing, A. J., D. W. Inouye, and R. B. Primack. 2008. How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *Journal of Ecology* 96:1289–1296.
- Morisette, J. T., A. D. Richardson, A. K. Knapp, J. I. Fisher, E. A. Graham, J. Abatzoglou, B. E. Wilson, D. D. Breshears, G. M. Henebry, and J. M. Hanes. 2008. Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. *Frontiers in Ecology and the Environment* 7:253–260.
- Nguyen, H. T., O. Kosheleva, V. Kreinvich, and S. Ferson. 2009. Trade-off between sample size and accuracy: case of measurements under interval uncertainty. *International Journal of Approximate Reasoning* 50:1164–1176.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Pau, S., E. M. Wolkovich, B. I. Cook, T. J. Davies, N. J. B. Kraft, K. Bolmgren, J. L. Betancourt, and E. E. Cleland. 2011. Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology* 17:3633–3643.
- Pereira, H. M., et al. 2013. Essential biodiversity variables. *Science* 339:277–278.
- Richardson, A., and S. Klosterman. 2015. Phenocam installation instructions. Available online at: [http://phenocam.sr.unh.edu/pdf/PhenoCam\\_Install\\_Instructions.pdf](http://phenocam.sr.unh.edu/pdf/PhenoCam_Install_Instructions.pdf)
- Richardson, A., and J. O’Keefe. 2009. Phenological differences between understory and overstory: a case study using the Long-Term Harvard Forest Records. Pages 88–117 in A. Noormets, editor. *Phenology of ecosystem processes*. Springer-Verlag, New York, New York, USA.
- Richardson, A. D., et al. 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3227–3246.
- Richardson, A. D., et al. 2012. Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program site synthesis. *Global Change Biology* 18:566–584.
- Schimel, D. S., et al. 2011. The National Ecological Network 2011 Science Strategy: enabling continental-scale ecological forecasting.
- Schwartz, M. D. 1998. Green-wave phenology. *Nature* 394:839–840.
- Schwartz, M. D., and J. M. Hanes. 2010. Intercomparing multiple measures of the onset of spring in eastern North America. *International Journal of Climatology* 30:1614–1626.
- Schwartz, M. D., R. Ahas, and A. Aasa. 2006. Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology* 12:343–351.

- Schwartz, M. D., J. L. Betancourt, and J. F. Weltzin. 2012. From Caprio's lilacs to the USA National Phenology Network. *Frontiers in Ecology and the Environment* 10:324–327.
- Schwartz, M. D., J. M. Hanes, and L. Liang. 2014. Separating temperature from other factors in phenological measurements. *International Journal of Biometeorology* 58:1699–1704.
- Singer, M. C., and C. Parmesan. 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3161–3176.
- Strode, P. K. 2003. Implications of climate change for North American wood warblers (Parulidae). *Global Change Biology* 9:1137–1144.
- Thibault, K. M. 2014. TOS science design for small mammal abundance and diversity. NEON document # NEON.DOC.000915. Available online at: <http://data.neoninc.org/documents>.
- U.S. Environmental Protection Agency. 2014. Climate change indicators in the United States, 2014. Third edition. EPA 430-R-14-004. [www.epa.gov/climatechange/indicators](http://www.epa.gov/climatechange/indicators).
- USA-NPN National Coordinating Office. 2012. Identifying and prioritizing data products and tools for use in science, management, and decision making. Research Coordination Network workshop report. USA-NPN Programmatic Series 2012-002. <http://www.usanpn.org>.
- White, M. A., D. Beurs, M. Kirsten, K. Didan, D. W. Inouye, A. Richardson, O. P. Jensen, J. O'Keefe, G. Zhang, and R. R. Nemani. 2009. Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982–2006. *Global Change Biology* 15:2335–2359.
- Willis, C. G., B. R. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable climate change response explains non-native species' success in Thoreau's woods. *PLoS ONE* 5:e8878.
- Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau, J. Regetz, T. J. Davies, and N. J. B. Kraft. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485:494–497.